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THE ARCHEGONIUM OF CATHARINEA ANGUSTATA BRID. (ATRICHUM ANGUSTATUM)

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(WITH PLATES I–VIII AND ONE FIGURE)

The archegonium of the Musci has been studied by numerous investigators, but the accounts of the developmental processes, especially the development and growth of the canal row, are so varied and even contradictory that the whole subject is in need of reinvestigation. *Catharinea* has been selected for an initial study because it is a representative of the most advanced group of the Musci. The results of studies of representatives of lower groups will appear later.

Material and methods

Catharinea is quite abundant in the region about Madison. The particular species here studied is *Catharinea angustata* Brid., as identified by Mrs. ELIZABETH G. BRITTON, to whom the author is greatly indebted for this courtesy. This entire investigation has been made on what is probably dioecious material. The sex organs were found not only on different gametophores, but these upright branches occur in relatively large, well defined patches or clusters of one sex or the other. A few cases were found in which the patch contained the upright branches of both sexes mixed together indiscriminately. The evidence here presented, while suggestive, is not conclusive of dioeciousness. An exact determination must await careful experimental work from spore to mature

plants. Abundant monoecious material, identified by Mrs. BRITTON as belonging to the same species, has been found at other stations, but this has been reserved for a later investigation.

Like many of the Musci, *Catharinea* displays evidence of being quite plastic. Thus plants taken from the same patch have shown striking variations in the number of lamellae; and even on different leaves of the same plant the number of lamellae may fluctuate beyond the limits given in taxonomic descriptions. The writer has little sympathy with the present tendency toward the manufacture of endless numbers of species on extremely slender bases. In regard to *Catharinea* careful investigations are needed to determine whether these minor differences are in reality specific, or are merely the fluctuations of a plastic form.

C. angustata forms archegonia rather early in the spring. Frequent collections were made at Eagle Heights, about 4 miles from the city, beginning the first week in April and ending the latter part of May. This was supplemented by other collections from stations on the campus and from Dorwood's Glen. The plants were transferred to large moist glass jars and almost daily killings made, thus securing a wealth of material for study. The killing agents used were 0.25 chrom-acetic and Flemming's medium. For the study of young stages serial paraffin ribbons were cut 5–6 μ; for the older stages 8–12 μ. As stains, safranin in combination with Licht Grün, Flemming's triple, and Heidenhain's iron alum hematoxylin were employed.

In staining moss material 10 μ or more in thickness the difficulty is often experienced that during the process some of the sections are almost certain to wash off, especially in the iron alum hematoxylin combination. This trouble was avoided through the use of a modification of the fixative devised by LAND (11). By experimentation the least possible amounts of gum arabic and chromic acid effective in 100 cc. of water were determined. Through the use of this there was no discoloration of the sections and staining was not interfered with. It was also found that standing the slides on end and allowing the excess fixative to drain off aids in preventing discoloration. CHAMBERLAIN (3, p. 114) states that this fixative will not keep. The writer, remembering a sug-

gestion once offered by LAND, has, in a well blackened bottle, fixative nearly a year old which is just as efficient as when first made up.

Historical

HOFMEISTER (6) in 1851 published the first account of the developmental processes in the archegonia of the Bryophyta. He examined a number of forms both among the Hepaticae and the Musci. In the latter group he found the antheridium and the archegonium exactly alike in the early stages of development, a fact which has been confirmed by subsequent investigations; but his account of the formation of the archegonium proper has received no confirmation from later workers. It is of interest therefore only from a historical standpoint. Among the Musci HOFMEISTER seems to have examined *Sphagnum*, *Phascum*, *Archidium*, *Funaria*, *Fissidens*, *Dicranum*, and *Polytrichum*.

In the early stages the growth is by an apical cell with two cutting faces. In each of the 2 cells thus formed there occurs a radial longitudinal division. The young archegonium now consists of 4 rows of cells. Then the formation of the archegonium proper takes place. In this process the cells of one of these longitudinal rows divide parallel to the outer wall, thus producing a central row of cells (the canal row) surrounded by 4 peripheral cell rows. Later 2 of these peripheral cells divide, thus completing the 6 cells of the periphery of the neck.

In 1858 SCHIMPER (12) published his historic monograph on *Sphagnum*. He describes the early stages in archegonial development as arising through the activity of an apical cell with 2 cutting faces, thus confirming the account given by HOFMEISTER. He is unwilling to commit himself in regard to the origin of the archegonium proper, however, referring the reader to HOFMEISTER's account in the mosses, which he is able neither to affirm nor to deny.

KÜHN's (10) interpretation of the development of *Andreaea* appeared in 1870. His account of the origin of the archegonium proper differs radically from that given by HOFMEISTER. He found that in the uppermost cell, which finally becomes the mother cell of the archegonium proper, 3 walls appear in such a way as to cut

out 3 peripheral segments and originate a central cell. The central cell now divides into an outer and an inner cell. The latter is the first cell of the axial row. The outer cell grows considerably, and again the 3 peripheral segments and the inner cell are cut off. The latter divides into an inner and an outer cell. Thus the second cell of the axial row arises just as did the first, and KÜHN holds that all subsequent cells of the axial row are produced in the same manner.

In 1872 JANCZEWSKI (9) made a study of the archegonia of several mosses. He names 2 species of *Sphagnum*, *Atrichum* (*Catharinea*) *undulatum*, *Bryum crudum*, *Funaria hygrometrica*, and *Phascum cuspidatum*. JANCZEWSKI's account of the development of these mosses is very brief. He mentions only the chief points, and gives no details. It is unfortunate also that the paper has no illustrations. In regard to *Atrichum undulatum*, *Bryum crudum*, *Funaria hygrometrica*, and *Phascum cuspidatum*, his chief points are as follows: There is development by an apical cell with 2 cutting faces, producing a few-celled structure which at this time cannot be distinguished from a young antheridium. In the uppermost cell, which is to be the mother cell of the archegonium proper, there now appear, just as KÜHN described for *Andreaea*, 3 oblique walls cutting off 3 peripheral segments and forming a funnel-shaped inner cell. This inner cell then divides to form an outer cell (the cover cell) and an inner cell. This last formed inner cell again divides, the lower cell being the ventral cell of the archegonium, while the upper cell is the primary neck canal cell. The cover cell continues to act as an apical cell, cutting off peripheral segments and canal initials. The number of canal initials varies from 2 to 6. The cover cell may cut off 1, 2, or 3 peripheral segments before forming a new canal initial. That is to say, there is no mathematical proportion between the cutting off of peripheral segments and canal initials. In the growth of the canal row the cells are of different origins. The upper cells arise through the cross divisions of the 2–6 canal initials, while the lower cells arise through the transverse divisions of the primary canal initial. The archegonium of *Sphagnum* is reported in general to show the same sort of development that has been described for the other mosses.

In 1884 HY (8) summarized the archegonial situation in the Musci as well as in other groups. His paper is noteworthy only for its philosophical considerations. In a very general way he confirms the findings of JANCZEWSKI, but adds little that is new or convincing to the subject.

In 1895 CAMPBELL (2, pp. 201, 202) studied the development of the archegonium of *Funaria hygrometrica*. Here the first division separates a basal cell from a terminal cell, which is the mother cell of the archegonium proper. "In the latter 3 walls now arise, as in the Hepaticae and *Andreaea*, but in *Funaria* they do not all reach the basal wall, but intersect at some distance above it, so that they inclose a tetrahedral cell, pointed below instead of truncate." The tetrahedral cell makes the usual division into "cover cell" and inner cell. The latter now divides, forming the primary neck canal cell and the ventral cell. "The cover cell instead of dividing by quadrant walls has a regular series of segments cut off from it and acts as an apical cell. These segments are cut off parallel both to its lateral faces and base and thus form 4 rows of segments, the 3 derived from the lateral faces forming the outer neck cells, and the row of segments cut off from the base constituting the axial row of neck canal cells." As to the further growth of the canal row, CAMPBELL states that the canal cells, "so far as could be determined, do not divide after they are first formed."

GAYET (4) in 1897 undertook a re-examination of the whole question of archegonial development in the Bryophyta, the investigation covering numerous forms both among the Hepaticae and the Musci. In the latter group, which alone interests us in the present discussion, he mentions 3 species of *Sphagnum*, 2 of *Andreaea*, and the following members of the Bryales: *Archidium*, *Ephemerum*, *Pleuridium*, *Phascum*, *Diphyscium*, *Barbula*, *Orthotrichum*, *Eucalyptra*, *Bryum*, *Mnium*, *Fissidens*, *Fontinalis*, and *Hypnum*. Summing up the main points of his study GAYET arrives at the following conclusions (p. 241):

1. L'archégone des Hépatiques se développe, non seulment par croissance intercalaire, mais encore par croissance terminale.

2. Chez les Mousses cette croissance terminale contribué fortement a l'allongement de l'organe femelle; il n'y a donc pas seulement 5 ou 6 segments.

3. La cellule terminale ne donne point de cellules de canal, pas plus chez les Mousses que chez les Hépatiques.

4. Les cellules de canal du col ont toutes la même origine; elles proviennent toujours d'une initale détachée de la cellule mère de l'oosphère; il n'y en a point d'adventives qui seraient formées aux dépens de la cellule terminale.

GAYET'S conclusions, therefore, are diametrically opposed to those reached by other investigators.

In 1898 GOEBEL (5) gives a rather brief and unsatisfactory account of his examination of *Mnium undulatum*. He states (p. 17): "I find in this plant confirmation throughout of the statements of JANCZEWSKI and others, and that the archegonium of the Musci is to be distinguished from that of the Hepaticae by its peculiar apical growth" (text fig. 1). The cell represented as apical in this figure is most certainly not the one described by JANCZEWSKI. GOEBEL'S illustration would lead us to believe that the canal row has been formed by the activity alone of the one cell marked +. This is most certainly not the method of canal row formation described by JANCZEWSKI. Hence GOEBEL must be regarded as giving an entirely different account for the development of the canal row.

FIG. 1.—Archegonium of *Mnium undulatum*, reproduced from GOEBEL'S *Organography, fig. 8, iv+*.

HOLFERTY (7) in 1904 made a critical study of the archegonium of *Mnium cuspidatum*. Here for the first time we have evidence somewhat scanty, but thoroughly convincing so far as it goes, because based on the sure foundation of division figures. In the development of the canal row HOLFERTY found once, and figures, the cover cell adding to the canal row. In 3 other archegonia he shows the topmost canal cell in the process of division, while in one case the basal neck canal cell is dividing.

Regarding the development of the archegonium proper his summary is as follows (p. 122):

6. In the young archegonium the 2-sided apical cell gives place to a 3-sided one which is truncate.

7. This terminal cell divides transversely soon after its formation giving rise to the first cell of the axial row.

8. The terminal cell adds to the growth of the neck by segments cut from its 3 lateral faces, and to the growth of the axial row by segments cut from its truncate face.

9. Growth in length of the archegonium neck is intercalary as well as apical in both neck and canal rows.

SERVETTAZ (13) in a quite recent physiological paper on the Musci includes an investigation of the development of *Phascum cuspidatum*. The developmental story is given briefly as follows (p. 171):

La cellule initiale se cloisonne transversalment et donne une cellule de peid, "a," et une cellule supérieure "b"; la cellule "b" se cloisonne ensuite obliquement un certain nombre de fois (2–5) comme s'il s'agissait de constituer un bourgeon végétatif ordinaire, puis l'une des cellules placées au-dessous de la cellule terminale se divise tangentiellement et détermine la formation d'une cellule central "c" qui, par des cloisonnements basipètes, donne une file de 8 cellules qui seront: 1–4, les cellules du canal; 5, la cellule du ventre; 6, l'oosphere. . . .

Quant à la cellule terminale, "s," elle peut continuer à se diviser et elle forme la calotte recouvrant l'extrémité du col.

En definitive, le mode de formation que nous venons de décrire se rapproche de celui que Goebel a décrit pour Mnium undulatum.

The evidence offered in support of this developmental story is certainly too meager and not sufficiently critical to be convincing. Moreover, the origin of the central cell, or first cell of the axial row, by a tangential division of one of the segments below the terminal cell is a revival of the HOFMEISTER conception which numerous subsequent investigations have failed to confirm, both in the Hepaticae and in the Musci. It would be nothing less than remarkable, therefore, to find the origin of the archegonium proper in *Phascum* fundamentally different from that of the other Musci.

In 1915 the author (1) published his studies on the archegonium of *Sphagnum subsecundum*. From sections both transverse and longitudinal it was shown that the archegonium proper is initiated in the terminal cell by the appearance of 3 oblique walls, which cut off 3 peripheral segments and produce the axial cell within. This latter cell on division gives rise to the cover cell and the central cell. Clear evidence is presented that the cover cell is relatively inactive, forming no basal segments, while division figures

make it certain that the growth of both canal row and peripheral cells of the neck is intercalary and not apical.

SUMMARY

In regard to the formation of the archegonium proper in the Musci 3 theories have been advanced: (1) the HOFMEISTER conception of the tangential division of one of the 4 original pedicel rows, a theory soon made untenable by the work of later investigators; (2) a recent revival of the HOFMEISTER scheme modified by the tangential division of one segment only, as proposed by SERVETTAZ; (3) the commonly accepted account, confirmed again and again for all the great groups of the Bryophyta, namely, the appearance in the terminal cell of 3 oblique walls forming 3 peripheral segments and an axial cell within.

It cannot be maintained, therefore, that the origin of the archegonium proper is in doubt. The evidence is too overwhelming to admit of any uncertainty on this point. However, the development of the axial row is another matter. Here is a subject involving widely conflicting accounts, some being diametrically opposed. Summarized, these accounts are: (1) the abandoned conception of HOFMEISTER, having only a historic interest; (2) KÜHN's claim for *Andreaea* that all the cells of the axial row are cut from the base of the apical cell; (3) CAMPBELL states for *Funaria* that the axial row is composed of a primary canal cell and segments cut from the base of the apical cell, none of which divide after they are formed, so far as could be determined; (4) GOEBEL holds that in *Mnium undulatum* the topmost neck canal cell (the one just below the cover cell) acts as an apical cell in the production of the canal row; (5) JANCZEWSKI finds that the cells of the axial row are of diverse origins, the upper arising through transverse divisions of the 2–6 initials cut from the base of the apical cell, while the lower are formed by the transverse divisions of the primary canal initial; (6) HOLFERTY has shown that the growth in the canal row of *Mnium cuspidatum* is both apical and intercalary; (7) GAYET concludes that the canal cells among the Musci have all the same origin, that there are no segments cut from the base of the apical cell, but that the whole axial row arises from an

initial produced by the mother cell of the egg; (8) SERVETTAZ states that in *Phascum* the canal row is formed by the basipetal divisions of the central cell; (9) the author has shown by division figures that in *Sphagnum subsecundum* the growth of the canal row is entirely intercalary.

It is evident that the Bryales are in need of a reinvestigation, not a superficial examination of many forms, but a careful intensive study of representative forms showing as far as possible by actual division figures the course of development. It is with such an idea in mind that the present work has been undertaken.

Development of archegonium

The apparently dioecious *Catharinea angustata* here studied produces a fairly large number of archegonia on each gametophore. The count shows variability with an average of about twenty. As previously stated, young archegonia begin their appearance early in April, and by the middle or end of May the majority have reached maturity. The first archegonium arises from the apical cell region, but whether from the apical cell itself or from one of its immediate segments cannot be stated positively at present. The study of the behavior of the apical cell in the production of archegonia and the continued growth of the gametophore, if fertilization does not occur, must be reserved for a later paper. In its early stages the archegonium develops by the usual method of an apical cell with two cutting faces (figs. 1, 3–5, 7–9). In the large amount of material examined only two exceptions to this statement have been found (figs. 2, 6). In both cases the young archegonia were developing in very crowded quarters, being closely surrounded by the stalks of archegonia nearing maturity.

After a variable number of segments, usually 4 or 5, have been produced by the apical cell, and secondary divisions have appeared in each segment except the terminal one, the plane of division changes. In the terminal cell, as so often described both for Hepaticae and Musci, 3 oblique walls cut off peripheral segments and originate the primary axial cell within. In fig. 10 the first oblique wall has been formed; in fig. 11 two of the oblique walls are shown. These oblique walls usually do not intersect, as CAMPBELL reports

for *Funaria*, but extend to the basal walls. The primary axial cell, therefore, has something of the shape of an inverted, truncated pyramid. There now follows the division of the primary axial cell into an outer axial cell, the cover cell, and an inner axial cell, the central cell (figs. 12, 13). Quite soon the central cell divides, the resulting lower cell being the ventral cell, while the upper is the primary neck canal cell (figs. 14, 15). The actual division of the central cell was found twice. The axial row of the young archegonium now consists of the ventral cell; its sister cell, the primary neck canal cell; and a large cover cell (figs. 15–17).

It is interesting to note that in fig. 15 the original division wall between cover cell and central cell appears tilted, due partly to the inequality in the growth of the peripheral segments, and partly to the change in the direction of the axis through the formation of new peripheral segments by the apical cell. While this tilting is not always found, it is of frequent occurrence, as shown to a greater or less extent in figs. 16, 18, 20, and furnishes valuable evidence in separating that portion of the axial row derived from the central cell from the part contributed by the cover.

The cover cell now cuts off peripheral segments (figs. 15–17). No absolute proof can be given as to their exact number, but it seems more than probable from such a series as figs. 15–18 that there are 3 peripheral segments. Then there is added to the canal row an initial cut from the base of the cover cell. The evidence for this statement rests on fig. 18, on several others quite like it, and is corroborated by the figures in the series about it (figs. 16–20). Several similar series could be constructed from the material studied. A long and careful search failed to reveal the actual division figure, but in fig. 18 the size and position of the nuclei and the delicate wall between leave no doubt that the uppermost canal cell has been cut from the base of the cover cell and that the process has just been completed. As illustrated by fig. 19 the axial row now consists of the ventral cell; its sister cell, the primary neck canal cell; an initial cut from the base of the cover cell; and a large cover cell or apical cell.

Up to this point the process of development is clear and definite; but from this point on there is a variability shocking to no

one save an old-fashioned, rigid morphologist. After the first initial has been added to the canal row, the apical cell again begins to cut off peripheral segments (figs. 20, 23), but in the meanwhile the periphery is also growing by intercalary divisions (figs. 19, 20, 22). While these peripheral processes are going on, the cells of the neck canal row are not inactive. The primary neck canal cell may divide first (figs. 20, 21), or the initial cut from the base of the cover cell may make the first division (fig. 22). That there are intercalary divisions in almost any order at this stage of the process may clearly be seen from the series represented by figs. 25–28. The archegonium has now reached the stage when it contains 4 or 5 neck canal cells. At this time the evidence is positive that the cover cell adds a second initial to the row of neck canal cells (figs. 29, 31). Fig. 29 illustrates excellently the intercalary as well as apical growth of the archegonium.

While fig. 31 is of interest in showing the activity of the cover cell in adding an initial to the canal row, it has an additional interest in giving evidence as to the origin of oblique walls in the axial row. The axis of the spindle is tilted and an oblique wall is being formed. In fig. 32 the process has been completed and the result is very evident. There are then two origins for the oblique walls in the canal row. The first we have mentioned in connection with fig. 15. No reliable evidence could be found that these walls might arise in any other way, such, for example, as the intercalary division of a canal cell. As a result of intercalary as well as apical activity the canal row now contains 5–7 canal cells. In the events that follow there is no definite sequence that can be determined. The only positive statement that can be made is that the number of canal cells is increased by intercalary divisions and in practically any order (figs. 33–45).

Just how active the cover cell is at this time cannot be stated, but the numerous figures in the canal row and the periphery of the neck make it evident that intercalary divisions are responsible in a large measure for the growth of the archegonium. In figs. 42, 44, it seems very probable that in each case the topmost canal cell has been cut from the base of the cover cell. No division figure could be obtained, so that a positive assertion cannot be made.

Fig. 48 shows the formation of what is probably in the majority of cases a last initial cut from the base of the cover cell. Abundant evidence has been found that at some time between the 12–16 neck canal cell stage the cover cell changes its manner of division and segments by a wall perpendicular to its base into two more or less equal parts (figs. 50, 51, 54, 56). The division figure was found once and is shown in fig. 56. No evidence could be obtained that the division may occur before the 12 neck canal cell stage; while after the 16 neck canal cell stage practically all covers showed division. Out of the large number of cases studied only two exceptions were found, one a case of 18 neck canal cells, and the other a case of 20 with the cover in each yet undivided. Such a process, then, while occurring within general limits is by no means fixed. Whenever such a division does occur, it signalizes the end of all true apical activity. The segmented cover stands out well defined from the peripheral segments of the neck and its history can be followed for some time with a reasonable degree of accuracy. Thus in figs. 61 and 62 the cover cell has formed 6 segments (3 shown in median longitudinal section) and is literally the cap of the archegonium. In fig. 72*A* we have the cross-section of the cover of an archegonium containing 35 neck canal cells. It shows clearly the primary division wall 1–1; the quadrant walls 2–2; and the subsequent divisions in each quadrant. When the archegonium is fully matured the segments of the cover merge insensibly with those of the neck, hence an exact statement cannot be made as to the final number produced.

The division of the ventral cell into ventral canal cell and egg was found five times, 3 being shown (figs. 47, 50, 53). Here again one finds the same sort of variability noted for the cover cell, but with a slightly greater range. The division may occur as early as the 11 neck canal cell stage (fig. 47), while several cases were found in which there were 17–20 neck canal cells with the venter yet undivided (figs. 58, 60). The ventral canal nucleus formed by this division is quite variable in size. Sometimes it is about the same size as the egg (figs. 56, 61, 68); or it may be noticeably smaller (figs. 54, 59, 62).

As already stated, the cutting off of initials from the base of the cover cell is in the majority of cases brought to a conclusion some-

where between the 12 and 16 neck canal cell stages; but since the undivided cover cell may be found as late as the 20 neck canal cell stage, it is evident that a variable number of initials may be cut from its base. We have given proof that at least 3 initials are produced, but we can make no positive statement as to the maximum number. By making due allowance for the rapid intercalary growth, we should estimate that in the majority of cases the number does not exceed 5 or 6.

Whatever may be the number of initials, the fact remains that both the canal row and the peripheral cells of the neck continue to grow by intercalary divisions. Figs. 45–61 show some of the many divisions found and furnish ample proof for the statement. This continued intercalary growth finally produces an astonishingly large number of neck canal cells. In the material studied the average count is well over 50; frequent examples in the sixties were found; two in the seventies (one with 74 and the other with 76 neck canal cells); and finally one example in which there were 86 neck canal cells with several of the basal neck canal cells just beginning to disintegrate. Not only is the number of neck canal cells large, but the canal row is generally multiple in its upper part (fig. 65). Less often this multiplicity is found through the middle portion of the neck (fig. 66) and in the basal part of the canal row (fig. 68). We have interesting evidence from fig. 64 that this multiple condition may arise by the simultaneous division of the cells concerned.

A study of cross-sections through mature archegonia furnished some interesting facts. A representative series through the terminal portion of the neck is shown in fig. 69*A–F*. The canal row is not merely double in this portion but generally consists of 3 cells and in some cases 4. The peculiar enlargement of the canal at its upper end is well shown by figs. 65, 69. The breaking down of the canal row in all of the cases observed was acropetal, but did not involve the ventral canal cell. This latter cell persists for some time, but its history up to fertilization has not been followed as yet. The venter of the mature archegonium is not uniform in thickness, but shows variations from 2 to 4 cells (fig. 63).

ABNORMALITIES.—In the large amount of material studied there was a striking lack of the so-called abnormalities. Only

two cases were found, one being illustrated in fig. 70. The archegonium here contains 17 neck canal cells, 3 of which are shown, and has 3 cells in the venter. It seems probable that the 2 lower ones were formed by the division of the egg, while the upper is the ventral canal cell which has remained undivided. Fig. 71 is the reconstruction of a very remarkable double archegonium. It may have originated by the fusion of 2 very young archegonia, or by the longitudinal instead of transverse division of the primary axial cell.

Discussion

Catharinea undulata has been studied by JANCZEWSKI only. The present work on the closely related *C. angustata* confirms in general his statements, especially in reference to the origin and development of the canal row. There can be no doubt that the cells of the neck canal row in *C. angustata* are of diverse origins. The lower arise through intercalary divisions of the primary neck canal cell, while the upper are produced by the intercalary divisions of at least 3 initials cut from the base of the cover cell.

Aside from the activity of the cover cell, there is no evidence that any *one* neck canal cell may act as an apical cell in the development of the canal row. On the contrary, the evidence is clear that *any* cell of the neck canal row may divide and in any order. This process is also in general agreement with the findings of HOLFERTY for *Mnium cuspidatum*, where both apical growth and intercalary divisions are reported. If CAMPBELL is correct, *Funaria* shows a striking difference, in that the primary canal cell and the initials cut from the base of the apical cell do not divide after they have been formed; while GOEBEL's account for *Mnium undulatum* shows still further difference, in that one of the neck canal cells at the apex of the canal row becomes an apical cell and by its activity produces the further growth of the canal row. If these differences are confirmed, we shall have a remarkably interesting series in archegonial development.

The facts in the present paper furnish an emphatic denial of the sweeping generalization of GAYET that among the Musci the cover cell does not give rise to neck canal cells. While the author has shown in a previous paper that in *Sphagnum subsecundum* no

initials are added to the canal row by the cover cell, this investigation makes it certain that in *Catharinea angustata* at least 3 initials are produced. Just what type of development the representatives of other groups of the Bryales will show remains to be seen.

Conclusions

The archegonium of *Catharinea angustata* grows for a time by apical as well as intercalary divisions in both canal row and peripheral cells of the neck. In its later stage the entire growth is intercalary.

The cells of the canal row have a double origin. The lower are formed by the intercalary divisions of the primary neck canal cell, the upper through the intercalary divisions of the 3 or more initials cut from the base of the cover cell.

How general this condition is among the Bryales must await further work.

Summary

1. The archegonia of *Catharinea angustata* begin to develop in April.

2. The first formed archegonium arises from the apical cell region, but whether fron the apical cell itself or from one of its immediate segments must be determined later.

3. In the earlier stages of development the young archegonium is formed by the activity of an apical cell with two cutting faces producing a filament of a few cells.

4. The archegonium proper is initiated by the appearance in the terminal cell of 3 oblique walls cutting off 3 peripheral segments and originating the primary axial cell within, which on division gives rise to the cover cell and the central cell.

5. The central cell on division forms the primary neck canal cell and the ventral cell.

6. The cover cell is active for a time, cutting off peripheral segments for the outer cells of the neck and basal initials for the canal row.

7. The number of basal initials varies, but is at least 3 in *Catharinea undulata*.

8. The cells of the canal row and the peripheral cells of the neck grow by intercalary divisions, and in any order.

9. The major growth of the archegonium is intercalary.

10. The cells of the neck canal row have a double origin. The lower are formed by the intercalary divisions of the primary neck canal cell; the upper through the intercalary divisions of the 3 or more initials cut from the base of the cover cell.

11. The ventral cell divides relatively early into ventral canal cell and egg.

12. The ventral canal cell is variable in size.

13. The mature archegonium has usually more than 50 neck canal cells, and may contain as many as 86.

14. The canal row is generally multiple in its upper part and occasionally throughout.

15. The disintegration of the canal row is acropetal, but does not involve the ventral canal cell.

16. If the number of neck canal cells is an indication of primitiveness, the most advanced group of the mosses has the most primitive archegonium yet described among the Bryophyta.

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LITERATURE CITED

1. BRYAN, GEO. S., The archegonium of *Sphagnum subsecundum*. BOT. GAZ. **59**:40–56. *pls.* 4–7. 1915.
2. CAMPBELL, D. H., Mosses and ferns. New York. 1905.
3. CHAMBERLAIN, C. J., Methods in plant histology. Chicago. 1915.
4. GAYET, L. A., Recherches sur le développement de l'archégone chez les Muscinées. Ann. Sci. Nat. Bot. VIII. **3**:161–258. *pls.* 7–13. 1897.
5. GOEBEL, K., Organography of plants. Oxford. 1905.
6. HOFMEISTER, W., Vergleichende Untersuchengen der Keimung, Entfaltung, und Fruchtbildung höherer Kryptogamen. Leipzig. 1851.
7. HOLFERTY, G. M., The archegonium of *Mnium cuspidatum*. BOT. GAZ. **37**:106–126. *pls.* 5, 6. 1904.
8. HY, F., Recherches sur l'archégone et le développement du fruit des Muscinées. Ann. Sci. Nat. Bot. VI. **18**:105–206. *pls.* 9–14. 1884.
9. JANCZEWSKI, E. VON, Vergleichende Untersuchungen über die Entwicklungsgeschichte des Archegoniums. Bot. Zeit. **30**:377–393, 401–417, 440–443. 1872.
10. KÜHN, E., Zur Entwicklungsgeschichte der Andreaeaceen. Schenk und Lürssen's Mittheil. aus dem Gesammtgebiete der Botanik. **1**:31. 1870.

11. LAND, W. J. G., Microtechnical methods. BOT. GAZ. **59**:397–401. 1915.
12. SCHIMPER, W. PH., Versuch einer Entwickelungsgeschichte der Torfmoose. Stuttgart. 1858.
13. SERVETTAZ, C., Recherches expérimental sur le développement et la nutrition des Mousses en milieux stérilisés. Ann. Sci. Nat. Bot. IX. **17**:111–223. *pls. 1–4.* 1913.

EXPLANATION OF PLATES I–VIII

All figures were drawn with the aid of Abbé camera lucida at table level, and, being reduced one-half in reproduction, now show the following magnifications: figs. 1–27, ×870; figs. 28–35, 64–68, ×700; figs, 36–44, 63, 69, 70, 72–74, ×550; figs. 45–62, ×410; fig. 71, ×225. Abbreviations are as follows: *a*, base of older archegonium; *l*, leaf; *p*, paraphysis.

PLATE I

FIG. 1.—First archegonium arising from apical cell region.

FIG. 2.—Young archegonium with abnormal cross walls arising at base of older archegonia.

FIG. 3.—Typical development by apical cell with 2 cutting faces.

FIG. 4.—The same, slightly older.

FIG. 5.—The same, still older.

FIG. 6.—Development by walls which do not quite intersect; bases of older archegonia seen on each side of young archegonium.

FIG. 7.—Typical development, older stage.

FIG. 8.—The same.

FIG. 9.—The same; relation to apical cell well shown.

FIG. 10.—First archegonium arising from apical cell region which has now segmented irregularly; in terminal cell the first of the 3 oblique walls originating the archegonium proper has been formed.

FIG. 11.—In terminal cell the 3 oblique walls have cut off peripheral segments and formed primary axial cell within.

FIG. 12.—Primary axial cell has divided into cover cell and central cell.

FIG. 13.—The same, slightly older.

FIG. 14.—Central cell dividing to form primary neck canal cell and ventral cell.

FIG. 15.—Division of central cell has just been completed; cover cell has formed a peripheral segment on the right.

PLATE II

FIG. 16.—Primary neck canal and primary ventral cell.

FIG. 17.—The same; cover cell has formed 3 peripheral segments, 2 being shown.

FIG. 18.—Two neck canal cells and ventral cell; topmost neck canal cell is the first initial cut from base of cover cell and has just been formed.

FIG. 19.—Two neck canal cells and ventral cell, later stage.

FIG. 20.—Two neck canal cells and ventral cell; cover cell forming a peripheral segment, while primary neck canal cell is in division.

FIG. 21.—Two neck canal cells and ventral cell; primary neck canal cell in division.

FIG. 22.—Two neck canal cells and ventral cell; first initial cut from base of cover in division.

FIG. 23.—Two neck canal cells and ventral cell; cover cell forming a peripheral segment.

FIG. 24.—Three neck canal cells and ventral cell.

FIG. 25.—Three neck canal cells and ventral cell; middle neck canal cell in division.

FIG. 26.—Three neck canal cells and ventral cell; topmost neck canal cell in division.

FIG. 27.—Four neck canal cells and ventral cell.

PLATE III

FIG. 28.—Four neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 29.—Four neck canal cells and ventral cell; simultaneous division of basal and topmost neck canal cell, while cover cell adds a second initial to canal row.

FIG. 30.—Four neck canal cells and ventral cell; cover cell forming peripheral segment.

FIG. 31.—Four neck canal cells and ventral cell; cover cell adding second initial to canal row.

FIG. 32.—Five neck canal cells and ventral cell; topmost neck canal cell cut from base of cover cell.

FIG. 33.—Five neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 34.—Five neck canal cells and ventral cell; topmost neck canal cell in division.

FIG. 35.—Five neck canal cells and ventral cell; basal neck canal cell in division.

PLATE IV

FIG. 36.—Six neck canal cells and ventral cell.

FIG. 37.—Six neck canal cells and ventral cell; topmost neck canal cell in division.

FIG. 38.—Seven neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 39.—Seven neck canal cells and ventral cell; fifth neck canal cell from ventral cell in division.

FIG. 40.—Eight neck canal cells and ventral cell; fourth and fifth neck canal cells from ventral cell in simultaneous division; topmost neck canal cell probably cut from cover cell.

FIG. 41.—Eight neck canal cells and ventral cell; basal canal cell in division; marked intercalary growth in the peripheral cells of the neck.

FIG. 42.—Nine neck canal cells and ventral cell; middle neck canal cell in division; topmost neck canal cell probably cut from base of cover cell.

FIG. 43.—Nine neck canal cells and ventral cell; fourth neck canal cell in division.

FIG. 44.—Nine neck canal cells and ventral cell; fourth and sixth neck canal cells from ventral cell in simultaneous division.

PLATE V

FIG. 45.—Ten neck canal cells and ventral cell; ninth neck canal cell in division.

FIG. 46.—Eleven neck canal cells and ventral cell; ninth and tenth neck canal cells in simultaneous division.

FIG. 47.—Eleven neck canal cells with ventral cell in division to form ventral canal cell and egg.

FIG. 48.—Eleven neck canal cells and ventral cell; cover cell adding an initial to canal row.

FIG. 49.—Eleven neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 50.—Twelve neck canal cells with ventral cell in division; cover cell has divided into 2 almost equal segments; apical activity ended.

FIG. 51.—Twelve neck canal cells, ventral canal cell, and egg; cover cell divided; apical activity ended.

FIG. 52.—Thirteen neck canal cells and ventral cell; ninth neck canal cell in division.

FIG. 53.—Thirteen neck canal cells with ventral cell in division; seventh, ninth, and tenth neck canal cells in division.

FIG. 54.—Thirteen neck canal cells, ventral canal cell and egg; eighth neck canal cell in division; cover divided.

PLATE VI

FIG. 55.—Thirteen neck canal cells and ventral cell; intercalary growth in peripheral cells of neck.

FIG. 56.—Fourteen neck canal cells, ventral canal cell and egg; ninth and tenth canal cells from ventral cell in division; cover cell dividing into 2 almost equal segments by wall perpendicular to base; apical activity now brought to an end.

FIG. 57.—Fourteen neck canal cells and ventral cell; ninth neck canal cell from ventral cell in division.

FIG. 58.—Eighteen neck canal cells and ventral cell; seventh and eighth neck canal cells from ventral cell in division; cover shows 3 segments in median longitudinal section.

FIG. 59.—Eighteen neck canal cells, ventral canal cell, and egg; eleventh and twelfth neck canal cells in division.

FIG. 60.—Twenty neck canal cells and ventral cell; fifth and sixth neck canal cells in division; peripheral cells showing intercalary divisions.

FIG. 61.—Thirty neck canal cells, ventral canal cell, and egg; 2 uppermost neck canal cells in division; cover shows 3 segments in median longitudinal section.

FIG. 62.—Forty-three neck canal cells, ventral canal cell, and egg; cover shows 3 segments in median longitudinal section.

FIG. 63.—Cross-section of venter of mature archegonium at level of egg, showing variable number of cells in thickness.

PLATE VII

FIG. 64.—Terminal portion of an archegonium approaching maturity with the 10 neck canal cells in simultaneous division.

FIG. 65.—Terminal portion of an archegonium approaching maturity showing marked enlargement of canal and multiple condition of canal row.

FIG. 66.—Middle portion of neck of an archegonium showing multiplication of neck canal cells.

FIG. 67.—Lower portion of an archegonium nearly mature showing 3 neck canal cells in simultaneous division.

FIG. 68.—Lower portion of an archegonium practically mature showing multiplication of canal cells; ventral canal cell and egg almost equal in size.

FIG. 69.—Series of transverse sections through terminal portion of a mature archegonium showing multiple condition of neck canal row.

PLATE VIII

FIG. 70.—Venter with 3 cells, 2 lowest are probably eggs; uppermost is probably ventral canal cell.

FIG. 71.—Double archegonium.

FIG. 72.—Serial sections through upper part of an archegonium containing 35 neck canal cells, ventral canal cell and egg; section *A* shows in cover cell: 1–1, primary division wall; 2–2, quadrant division; and further division in each quadrant; series shows variations in number of peripheral cells of neck.

FIG. 73.—Serial sections through middle portions of neck of same archegonium showing remarkable regularity in number of peripheral cells of neck.

FIG. 74.—Serial sections through lower portion of same archegonium showing thickness just above venter (*A–D*); venter at level of ventral canal cell (*E*); venter at level of egg (*F*).